

# What is Dental Ecology?

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**ABSTRACT** Teeth have long been used as indicators of primate ecology. Early work focused on the links between dental morphology, diet, and behavior, with more recent years emphasizing dental wear, microstructure, development, and biogeochemistry, to understand primate ecology. Our study of *Lemur catta* at the Beza Mahafaly Special Reserve, Madagascar, has revealed an unusual pattern of severe tooth wear and frequent tooth loss, primarily the result of consuming a fallback food for which these primates are not dentally adapted. Interpreting these data was only possible by combining our areas of expertise (dental anatomy [FC] and primate ecology [MS]). By integrating theoretical, methodological, and applied aspects of both areas of research, we adopted the term “dental ecology”—defined as the broad study of how teeth respond to the environment. Specifically, we view

dental ecology as an interpretive framework using teeth as a vehicle for understanding an organism’s ecology, which builds upon earlier work, but creates a new synthesis of anatomy and ecology that is only possible with detailed knowledge of living primates. This framework includes (1) identifying patterns of dental pathology and tooth use-wear, within the context of feeding ecology, behavior, habitat variation, and anthropogenic change, (2) assessing ways in which dental development and biogeochemical signals can reflect habitat, environmental change and/or stress, and (3) how dental microstructure and macro-morphology are adapted to, and reflect feeding ecology. Here we define dental ecology, provide a short summary of the development of this perspective, and place our new work into this context. *Am J Phys Anthropol* 148:163–170, 2012. © 2012 Wiley Periodicals, Inc.

Ecology is: “the total relations of the animal to both its organic and inorganic environment” and “above all, its...relations with those animals and plants with which it comes directly or indirectly into contact”

(Haeckel, 1866)

A niche: “indicate(s) what it (an animal) is doing and not merely what it looks like...”

(Elton, 1927)

For over two millennia, teeth have been a focus of attention when interpreting the behavior, ecology, and adaptations of living and extinct animals, including primates, other mammals, and other vertebrates (see reviews in Hillson, 1986, 2005; Teaford, 2000; Ungar, 2010). For example, scholars dating as far back as Aristotle observed that teeth are key in determining what an organism eats, thereby providing a correlate of an animal’s ecology and thus its niche (as defined by Elton, 1927) within a community (see Hillson, 1986; 2005; Ungar, 2010). Ungar (2010), describes Cuvier’s “axiom” of two centuries ago—“show me your teeth, and I will tell you who you are”—which reflects the importance of assessing teeth in an ecological context. Following early work, scholars ranging from Charles Darwin to numerous contemporary scientists have focused on teeth and their ecological implications (see Ungar, 2010). For example, Darwin, in describing the dental morphology of an extinct Neotropical mammal, wrote in his diaries in 1833: “The teeth indicate, by their simple structure, that these Megatheroid animals lived on vegetable food, and probably on the leaves and small twigs of trees” (Quammen 2009, p 52). This observation, of course, built on the work of earlier scholars. From these earlier, basic

studies to recent, more technologically driven research on tooth wear, development, structure, and biogeochemistry, teeth remain central to studies in anthropology, primatology, vertebrate paleontology, mammalogy, and many others academic areas.

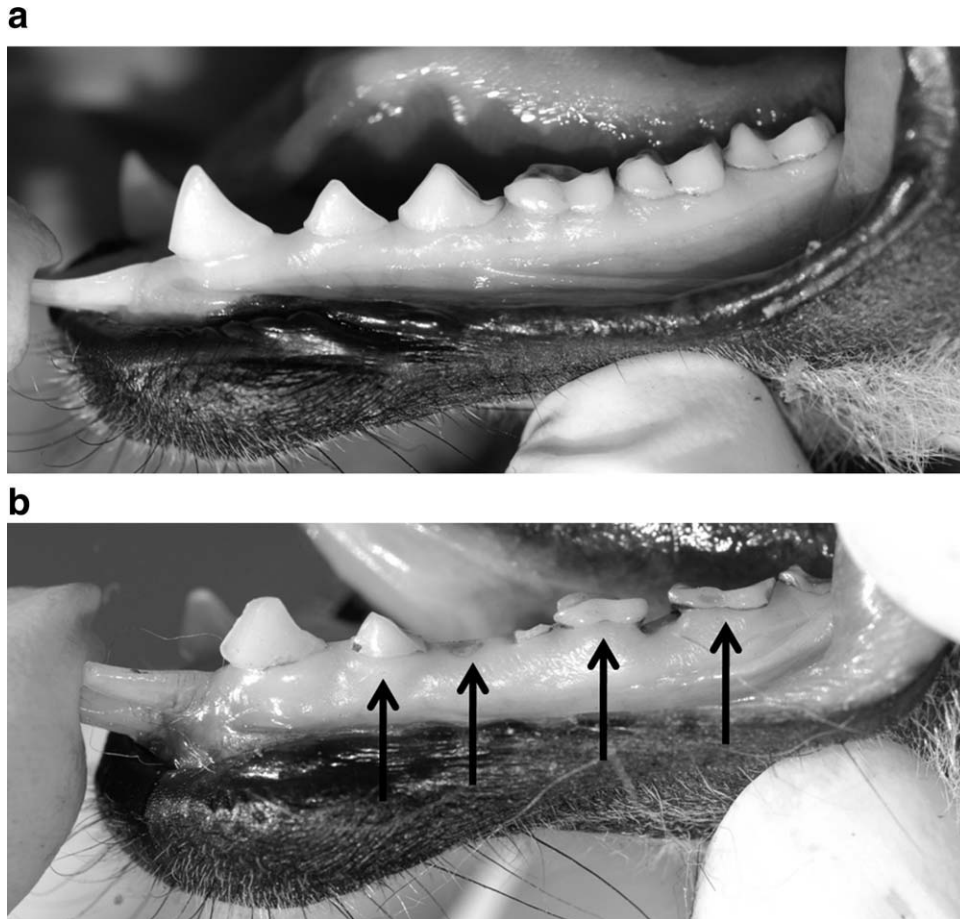
Teeth are the only part of the skeleton that make direct contact with the world outside of an organism, recording an organism’s growth and development (e.g., Schwartz and Dean, 2000), and providing an accurate record of that organism’s interaction with its environment. Teeth are central for understanding an organism’s life history and ecology. They provide insight into nutritional stress during ontogeny, as seen in the presence and/or frequency of enamel hypoplasia (e.g., Guatelli-Steinberg, 2001). They provide microwear features as a record of the most recent foods eaten (e.g., the “last supper” effect [Grine, 1986]). They offer hard tissue evidence of environ-

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**Fig. 1.** BMSR *Lemur catta* tooth wear: (a) limited wear in lemur no. 307, left mandibular tooth row; (b) severe wear and antemortem tooth loss, marked by arrows, in lemur no. 375, left mandibular tooth row.

mental change and/or habitat degradation as indicated by specific patterns of overall or “gross” wear (e.g., Cuozzo and Sauther, 2006; Sauther and Cuozzo, 2009; Jablonski and Leakey, 2008; Jablonski et al., 2008). They can also show how teeth are adapted to feeding ecology through the structure of enamel, its quantity, and arrangement (e.g., Constantino et al., 2009, in press). Thus, teeth provide a record of an organism’s ecology—i.e., its “total relations” with the overall environment (Haeckel, 1866)—and how that organism (and its ancestors) responded to its environment. This perspective spans the primate order, and includes an understanding of how modern human tooth-use wear and pathology reflects cultural traditions and changes in technology, for example, as seen in differences in tooth-use wear between agriculturalists and hunter gatherers (e.g., Smith 1984).

#### DENTAL ECOLOGY DEFINED

The term “dental ecology” rarely occurs in the academic literature, and when it does it is tied to mandibular morphology (e.g., Vaughn, 1970), or more recently to dentistry, to provide an environmental context for providing oral health and dental services (see <http://www.dentistry.unc.edu/depts/ecol/>). We define dental ecology as the broad study of how teeth respond to the environment. By respond, we mean how the environment shapes teeth, whether through natural selec-

tion (e.g., tooth size and morphology), or during the life of an animal, through wear, pathology, and/or development. As we argue herein, such study is only possible with comprehensive ecological data from living primates. Thus dental ecology includes: (1) identifying patterns of dental pathology, such as abscessed teeth, tooth loss, dental damage, and tooth use-wear, as these reflect feeding ecology, socio-ecology, habitat variation, and anthropogenic effects, (2) assessing ways in which dental development, including stable isotope signatures recorded in developing teeth, can reflect migration, environmental change and/or stress, and habitat use, and (3) how dental structure, specifically enamel properties, but also macro-morphology, are adapted to, and reflect, feeding ecology.

Why a new term? It’s clear that teeth have long been used to interpret and assess ecology in living and fossil primates. However, much of the history of primate dental study has focused on the relationships between morphology, tooth-use wear and diet, often with limited information on the actual ecology and behavior of living primates. With the increasing frequency of detailed, long-term ecological data for many primate species and/or populations, it is now possible to use teeth to directly assess ecological impacts on primate populations.

Does this mean that all work on primate teeth falls under the rubric of dental ecology? As we define the term, the answer is no. We specifically refer to dental ecology as the use of teeth to understand primate ecology

in the context of comprehensive ecological data on living primates. We began using the term “dental ecology” in 2007 (Cuozzo and Sauther, in press), specifically in reference to the dramatic pattern of severe tooth wear and antemortem tooth loss in the population of ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve (BMSR), Madagascar, which we have documented in detail elsewhere (Sauther et al., 2002, 2006; Cuozzo and Sauther, 2004, 2006; Cuozzo et al., 2008, 2010; Sauther and Cuozzo, 2009; see Fig. 1). This pattern of tooth-use wear clearly reflects this population’s interaction with their environment (e.g., their ecology), and as we have explained in many of these earlier publications, it is largely a result of consuming a physically and mechanically challenging fallback food, in a habitat which has experienced significant anthropogenic alteration (e.g., Sauther and Cuozzo, 2009; see Yamashita et al., in press; Cuozzo et al., submitted). However, without the now nearly 25 years of ecological and behavioral data collected by MS, and the decade-long dental study by FC, this assessment would not have been possible. This work also shows that detailed knowledge of feeding ecology, combined with data on dental gross wear, provide an important and until the past decade, understudied area of analysis (e.g., Ungar, 2002). Philips-Conroy et al. (2001) argue that patterns of gross wear reflect the long-term interactions of an organism with its environment. We suggest that in contrast to microwear studies, which present a “snapshot” of an animal’s interaction with its environment, studies of gross wear provide a “whole organism” perspective when tied to a long-term understanding of ecology and behavior. Such studies are now becoming more frequent especially with advanced techniques for the quantitative assessment of gross tooth wear (e.g., King et al., 2005; Ungar, 2007).

There are now demographic, ecological, and reproductive data from a growing number of long-term primate research projects (e.g., King et al., 2005; Leigh et al., 2008; Galbany et al., 2011) making it possible to integrate detailed dental data within an ecological context. For example, a study of *Propithecus edwardsi* at Ranomafana National Park, Madagascar, a site where this species has been studied for over two decades, indicates that female reproductive success corresponds to overall tooth wear (King et al., 2005). In this lemur population, reduced infant survival correlates with periods of reduced rainfall among mothers with advanced stages of tooth wear (King et al., 2005; Wright et al., 2008). Similarly, a long-term study (over 20 years) of *Mandrillus sphinx* at the Centre International de Recherches Médicales de Franceville, Gabon convincingly shows that male reproductive fitness co-varies with maxillary canine growth and wear (Leigh et al., 2008). A third recent example is seen in comparative work on food properties and dental morphology in living hominoids. The relationship between enamel thickness and food mechanical properties in extant chimpanzees and orangutans indicates that the fallback foods actually consumed by orangutans are indeed harder and thus more mechanically challenging than those of chimpanzees (Vogel et al., 2008). A final example of understanding primate ecology through teeth as part of long-term ecological research is seen in Galbany et al. (2011). This work on known-aged baboons (*Papio cynocephalus*) from Amboseli, Kenya, some more than 20 years old, demonstrates that interproximal tooth-wear and thus mesiodistal distance are directly impacted by age, which has implications for

assessing metric variation in extant and fossil primate samples. Such studies represent the core of our dental ecology perspective—interpreting and assessing primate ecology and behavior through teeth in the context of comprehensive information on living primates, and which also provides a framework for interpreting the ecology and behavior of fossil forms.

In this brief article, we present several examples of how a dental ecology approach can be an informative perspective for understanding primate ecology and paleoecology. Specifically, we highlight two areas where the dental ecology approach can be especially useful, integrating our previous work with new data expanding beyond our focal species (*L. catta*), and highlighting examples from the work of others, on both living and fossil primates.

### TEETH AS INDICATORS OF HABITAT CHANGE/ALTERATION

One of our major research goals is assessing whether the dramatic pattern of tooth-use wear and subsequent tooth loss we have previously described among the BMSR ring-tailed lemur population is an anomaly, and whether our dental ecology framework can be applied beyond our initial research species and/or areas, in terms of understanding the impact of anthropogenic effects on primate dental health. To further assess and interpret the pattern of ring-tailed lemur dental ecology at BMSR, we recently examined the skeletal collection of sympatric *Lepilemur leucopus* (the white-footed sportive lemur) housed at the reserve. As seen in Table 1, the skeletal sample of ring-tailed lemurs housed at BMSR displays a significantly higher frequency ( $P = 0.0262$ ) of antemortem tooth loss than sympatric sportive lemurs, in which not a single specimen displays this pattern. What does this mean from an ecological perspective? BMSR *L. leucopus* is a small (~600 g), nocturnal, dedicated folivore (Nash, 1998). In contrast, BMSR *L. catta* is best described as an opportunistic omnivore, with a broad, seasonally influenced diet that includes varied fruits, flowers, leaves, terrestrial herbs, invertebrates, and geophagy (e.g., Sauther, 1992, 1998; Sauther and Cuozzo, 2009). As such, BMSR ring-tailed lemurs often consume a series of physically, and mechanically challenging foods, dominated by, but not limited to tamarind fruit (Yamashita et al., in press). As we discuss above and elsewhere, BMSR ring-tailed lemurs consume endemic, possibly endemic (e.g., tamarind fruit), and clearly introduced foods (LaFleur and Gould, 2009; Sauther and Cuozzo, 2009). In contrast, sportive lemurs are arboreal, and even in areas outside of the protected BMSR reserve (where several of the cranial specimens were recovered), there are numerous tamarind trees that provide them with the young and mature leaves commonly consumed by this species (Nash, 1998). Sportive lemurs at BMSR also feed on numerous arboreal vines and euphorbs (Nash, 1998), which frequently remain available in degraded areas outside the protected reserve (Whitelaw, 2010). It therefore appears that recent habitat change, marked by anthropogenic effects, including removal of ground plants and the introduction of new plant species, leaves a notable anatomical marker in some but not all primate species at this site. In this case, severe tooth wear and antemortem tooth loss in this ring-tailed lemur population contrasts with sympatric sportive lemurs, who consume a variety of plants

TABLE 1. Comparison of dental pathology between *Beza Mahafaly Lemur catta* and *Lepilemur leucopus*, from the Beza Mahafaly Osteological Collection

Pathology	<i>n</i> = <i>Beza Lepilemur</i> n w/pathology	<i>n</i> = <i>Beza Lemur</i> n w/pathology	chi-square	<i>P</i> -value <sup>a</sup>	DF
Tooth loss	0/14	8/28	4.941	0.0262	1
Abscess	2/14	4/28	0.000	>0.9999	1

<sup>a</sup> Significant *P* values (*P* < 0.05).

TABLE 2. Comparison of greater galago (i.e., *Otolemur* = *Galago*) canine pathology/damage across intact (Balovale) and anthropogenically altered (Pemba) habitats

Pathology	<i>n</i> = Pemba n w/pathology	<i>n</i> = Balovale n w/pathology	chi-square	<i>P</i> -value <sup>a</sup>	DF
Broken/damaged	8/27	0/18	6.486	0.0109	1
Abscessed/decayed	7/27	0/18	5.526	0.0187	1

<sup>a</sup> Significant *P* values (*P* < 0.05).

but emphasize plant parts (i.e., leaves) that do not produce dental damage and which can be found within both intact and altered landscapes. Thus, a dental ecology approach demonstrates how different biological and environmental responses of sympatric species are reflected in their teeth.

#### Dental pathology in greater galagos—the impact of anthropogenic change

Although Madagascar's lemurs dominate our work with living primates, the dental ecology approach is not taxon specific. Using skeletal data on two wild-caught greater galago species (*Otolemur crassicaudatus* and *Otolemur garnetti*) collected in eastern Africa and curated at the Natural History Museum (London) and the American Museum of Natural History (New York), we have found that habitat effects leave a hard tissue signal for these species as well. Specimens come from Pemba Island, Tanzania (*G. garnetti*) and Balovale District, Zambia (*G. crassicaudatus*), and were collected in 1954–1955 (Masters et al., 1988; Lumsden, 1995). The area on Pemba Island where these individuals were collected is dominated by plantations (clove, coconut, and kapok—*Ceiba pentandra*), with small areas of grassland and forest (Masters et al., 1988; Lumsden, 1995), while specimens collected from Balovale are from a higher altitude (~1,000 m) plain dominated by “miombo” woodland, areas of dense forest and only scattered cultivation (Masters et al., 1988). Thus, these two locations displayed (in the 1950s) quite different levels of anthropogenic impact. A previous study (Masters et al., 1988), using this material found significant differences in the frequency of broken teeth between the two samples, with over 14% of the Pemba Island galagos having broken teeth, compared with less than 2% from Balovale displaying this pathology. The authors linked this to differences in diet at the two sites (Masters et al., 1988).

We examined these two samples for evidence of maxillary canine abscesses/decay, as this pathology correlates with anthropogenic effects seen in BMSR ring-tailed lemurs (Sauther et al., 2006). As seen in Table 2, the Pemba Island skeletal sample (*n* = 27) displays high frequencies of broken/damaged (29.6%) and decayed/abscessed (25.9%) maxillary canines (Fig. 2). In contrast, the Balovale sample (*n* = 18) exhibits neither of these dental patterns. As we note above, the Pemba Island

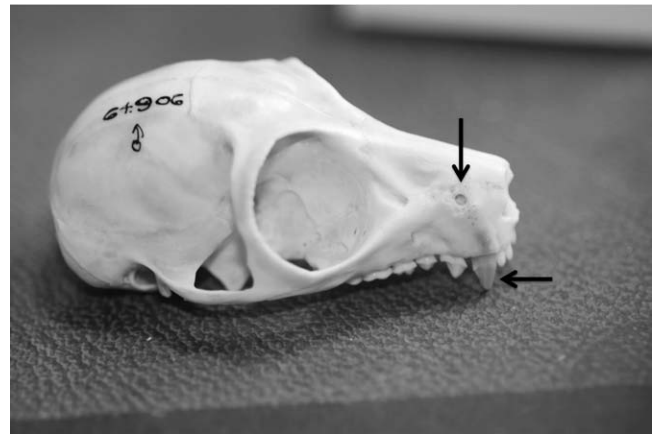


Fig. 2. Arrows show an apical maxillary canine abscess and decayed tooth in a greater galago (*Otolemur garnetti*) from anthropogenically altered habitat in Tanzania (Natural History Museum, London, BMNH specimen no. 64:906).

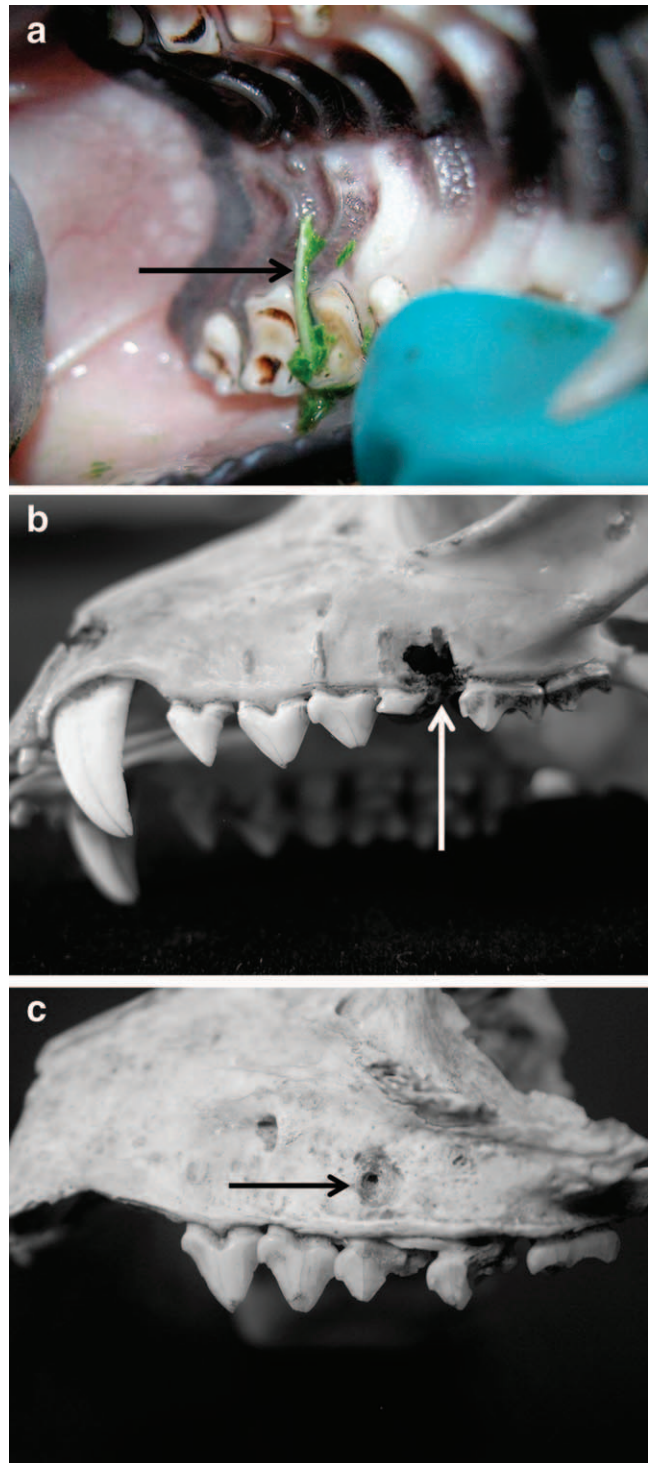
sample comes from an area of intense agricultural development, including coconut, clove, and kapok plantations (Lumsden, 1995). Dietary data for these two samples, based on analyses of their stomach contents, indicate that while both species exhibit a diet of approximately 50% invertebrates, the two samples differ in that the Pemba Island galagos were also consuming cultivated foods, including mango and coconut (Masters et al., 1988). At Balovale, *O. crassicaudatus* consumed a high proportion of gums, and a reduced frequency of fruit. The pattern of dental pathology (both broken teeth and abscesses) in the Pemba Island galagos can be explained as a product of these primates living in an area with notable human impact, leading them to consume physically challenging foods such as coconuts. In contrast, the Balovale galagos display none of the patterns of tooth breakage or the abscesses seen at Pemba Island, and lived in an area with far less anthropogenic change and with no evidence of consuming domestic plant foods. These two samples each display a dental ecology signal, respectively, reflecting the level of anthropogenic effects, in a pattern similar to that seen among BMSR ring-tailed lemurs, where maxillary canine abscesses correspond with areas of human degraded habitats (Sauther et al., 2006).

### TEETH AS A TOOL FOR INTERPRETING PALEOECOLOGY

An important goal of primate evolutionary biology is to elucidate the lifeways of extinct primates. Inherent in this goal is an emphasis on the relationships and adaptations of these extinct animals, largely based on the comparative method, the principal analytical method of evolutionary biology. In primate evolutionary biology, this method emphasizes the comparison of extinct primates with those extant primates, or analogs, that exhibit functional similarities to a respective fossil taxon (Kay and Covert, 1984; Anthony and Kay, 1993). Therefore, in order to fully understand the ecology of recent and more distant extinct forms, it is imperative to have as complete an understanding of extant primates as is possible, including detailed knowledge of their anatomy, adaptations, and ecology. In this context, teeth are especially useful for assessing paleoecology as they are the most frequently preserved remains in the vertebrate fossil record (e.g., Shipman, 1981).

As noted in our introduction to this article, the use of teeth to understand and interpret the ecology and behavior of extinct forms has a long history in primate biology. For example, the presence of male-biased canine dimorphism in early Tertiary primates has been suggested as evidence that these primates lived in polygynous social groups, and exhibited inter-male competition (Fleagle et al., 1980; Gingerich, 1981). This interpretation is, of course, based on patterns of canine dimorphism and their correspondence with multi-male/multi-female social systems in numerous extant primates. How does a dental ecology perspective further advance this question? Central to dental ecology is the synthesis of long-term data on living primates with dental studies. For example, work on mandrills showing that canine growth and wear correspond to male fitness in mandrills (Leigh et al., 2008) can also provide a framework for a more comprehensive analysis of sexual dimorphism and behavioral ecology in fossil primates. Specifically, these data suggest that life histories, including male reproductive fitness, can be elucidated through analyses of canine growth and wear in the fossil record (Leigh et al., 2008), which goes far beyond basic suggestions of polygynous mating systems.

A recent and increasingly common method of interpreting past behavioral ecology comes from stable isotope analyses of dental enamel, most notably in fossil hominins (e.g., Sponheimer and Lee-Thorp, 2007). The foods an organism eats, and the habitat in which that organism lived while its teeth were developing, leave a permanent isotopic signal that is preserved in the dental enamel and can be ascertained using biogeochemical methods (e.g., Copeland et al., 2011). By determining the connection between diet and isotopic signals in living animals it is now possible to apply this to expanding our understanding of earlier hominin diets. For example, we now know that despite a dental morphology consistent with hard object feeding, including large molars and extremely thick dental enamel, stable isotopes (carbon) from dental enamel indicate that *Paranthropus boisei* likely fed on foods such as grasses or sedges, rather than hard objects (Cerling et al., 2011). This is an excellent example of how new techniques that go beyond earlier, basic studies of dental morphology can provide important new interpretations of fossil primate ecology when linked to data from animals with known ecologies. Such



**Fig. 3.** (a) Arrow notes a leaf stem embedded between two maxillary molars in a living ring-tailed lemur at the Beza Mahafaly Special Reserve, Madagascar (BMSR lemur no. 245). (b) Arrow notes an abscessed and decayed maxillary first molar in a recent ring-tailed lemur skeletal specimen (Museum of Comparative Zoology, Harvard University specimen no. 16392); (c) Arrow notes an apical maxillary molar abscess in a subfossil ring-tailed lemur from Ankilitelo, Madagascar (Duke University Primate Center specimen no. 18753). [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]

approaches can even provide data on the social behavior of fossil hominin species. Copeland et al. (2011) have used stable isotope (strontium) values from two fossil hominin species, *Australopithecus africanus* and *P. boisei*, to suggest that differences in strontium values between what are thought to be male and female individuals (based on the degree of sexual dimorphism in these early forms) indicate males have smaller home ranges, and possibly were philopatric, i.e., stayed in their natal troops. In contrast, their data suggest that females migrated from their original troops, similar to extant chimpanzee species, *Pan troglodytes* and *Pan paniscus* (Copeland et al., 2011). This example further illustrates how a dental ecology approach, using the comparative method and information from living forms, can transcend temporal boundaries, and use extant forms to understand even complex ecological and behavioral aspects of fossil species through teeth.

An example from our own work also illustrates this point. Figure 3a shows a BMSR ring-tailed lemur with a leaf stem embedded between the first and second maxillary molars. Left in place, as would happen under natural conditions, this type of dental debris could easily lead to infection, dental and alveolar decay, and potentially apical abscesses. Figure 3b presents an image of maxillary molar decay and/or abscesses in a skeletal specimen from an extant ring-tailed lemur collected in southwestern Madagascar early in the 20th century (MCZ 16392), and Figure 3c shows a “subfossil” ring-tailed lemur specimen from the Ankilitelo Cave site (DUPC 18753), a locality preserving a fossil mammalian community, including a number of extant and extinct “giant” lemur specimens, dating to approximately 500 years BP (e.g., Muldoon et al., 2009; Muldoon, 2010). By comparing these patterns of pathology between extant and recent subfossil specimens, in the context of actual feeding and dental health data in a known, living lemur, we can provide a potential explanation for this pathology in a subfossil specimen of an extant form, including the types of foods this long-dead animal likely consumed. As noted, the Ankilitelo Cave sample dates to ~500 BP, and represents one of the most recent faunal assemblages in Madagascar containing both extant and the recently extinct “giant” lemurs (e.g., Muldoon et al., 2009; Muldoon, 2010). This locality, on the Mahafaly Plateau, sits in an area dominated by spiny forest. However, this plateau is frequently cross-cut by ephemeral and some permanent rivers. Along the waterways, there are areas of riverine gallery forest, marked by deciduous forest, similar to that found in the eastern portion of the Beza Mahafaly Special Reserve. The presence of this pathology in at least one specimen in the Ankilitelo ring-tailed lemur sample—among 38 total specimens, with a minimum number of 16 individuals—suggests that these ~500 BP ring-tailed lemurs were consuming at least some deciduous leaves. Thus, comparing dental health and pathology from living primate samples can inform questions of feeding ecology and habitat use in recent, and potentially more distant fossil primates.

### Dental ecology and past environmental change

We argue that a dental ecology approach can be used to assess and understand both natural and human-caused environmental change, particularly among living primate populations. However, teeth can also inform

questions of habitat and/or environmental change in the fossil record. One striking example comes from the Plio-Pleistocene of East Africa. Jablonski and coworkers (Jablonski and Leakey, 2008; Jablonski et al., 2008) describe a pattern of frequent, severe gross tooth wear, with teeth often worn to the roots, in *Cercopithecoides kimeui*. This large colobine monkey’s temporal range spans the boundary of the Pliocene and Pleistocene Epochs. Among specimens from Koobi Fora, the majority shows heavily worn maxillary and mandibular post-canine teeth (Jablonski et al., 2008). In addition, this heavy wear is described as occurring “early in life” (Jablonski et al., 2008, p 67), and suggests a diet rich in abrasive foods (e.g., roots and tubers), and more abrasive than another member of the genus, *Cercopithecoides williamsi*.

How does a dental ecology perspective help explain this interesting pattern of gross tooth wear? One of the major environmental changes seen across the Plio-Pleistocene boundary in East Africa is an intensification of seasonality, occurring approximately 1.80 mya, corresponding to greater aridity and declining vegetation (Leakey, 1982; Jablonski and Leakey, 2008). At this time, all of the large East African colobines became extinct, with only *C. kimeui*’s temporal range extending into the Pleistocene, as late as 1.58 mya (Jablonski et al., 2008). What is striking is that this species displayed its pattern of frequent severe tooth wear prior to its extinction. Given its thin-enameled, bilophodont molars, Jablonski and Leakey (2008, p 411) describe its dentition as being “poorly adapted to diets rich in highly abrasive grass phytoliths and other abrasives.” This indicates that this species was consuming foods for which its dentition was not morphologically adapted, in a changed environment of increasing aridity, etc., which is similar to what we describe for BMSR ring-tailed lemurs (Cuozzo and Sauther, 2006; Sauther and Cuozzo, 2009), albeit resulting from a recent, human-induced environmental change. From a dental ecology perspective, *C. kimeui* provides another example of how a broad, ecological perspective, including information from living primate populations, is necessary to understand the behavioral ecology of extinct primates.

### CONCLUSIONS

As noted by Elton (1927), an organism’s niche—its place in an ecological community—reflects what an animal does, not what it looks like. In this case, teeth can be viewed in a similar way—it is not simply how they look (i.e., their occlusal morphology) but what teeth do across the lifetime of individuals. Among the BMSR ring-tailed lemurs, dental morphology is consistent with folivory (e.g., Yamashita, 1998; Cuozzo and Sauther, 2006). Yet, at this location, a large, hard and tough fruit provides the primary fallback food for this species. Despite having “folivore” teeth, in this habitat ring-tailed lemurs often rely on a challenging fruit. It has only been through combining our different perspectives, i.e., using a dental ecology approach across multiple habitats, that we have been able to understand this anomaly. We thus argue that a thorough comprehension of primate ecology requires an approach that goes beyond dental morphology. While an understanding of dental morphology provides an excellent first approximation of ecology and behavior among both living and fossil forms, especially in the context of feeding, it is now possible to take

advantage of long-term primate studies to develop a deeper understanding of how teeth reflect an organism's environment, especially in the context of the rapid environmental change being faced by many extant primate communities.

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